THE PERMIAN CORAL *NUMIDIAPHYLLUM*: NEW INSIGHTS INTO ANTHOZOAN PHYLOGENY AND TRIASSIC SCLERACTINIAN ORIGINS

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ABSTRACT. The Permian coral *Numidiaphyllum*, having an unusual septal arrangement and an aragonitic skeleton, has been classified in the Rugosa. The type species of *Numidiaphyllum* shows high intraspecific morphological variability and distinct granulation on septal faces. Ontogenetic development indicates that corallites show hexameral septal arrangement and cyclic mode of insertion. The genus has no specific morphologies that deny scleractinian affinities. *Numidiaphyllum* is believed to have originated in sponge-algal reefs in the Permian tropics but possesses a basic scleractinian form which was already established in Early Palaeozoic times. Whatever their variation might be, the zoantharians, which may be closely related to *Numidiaphyllum*, survived the end-Permian extinction in 'deep-water' refuges as Permian holdovers, retaining their body plan, and they are possible scleractinian ancestors in the Triassic. Scleractinia have no immediate phylogenetic relationship to Rugosa. This study provides evidence about Permo-Triassic anthozoan phylogeny in terms of Permian survivors and their relationship to Triassic scleractinian origins.

CNIDARIA are among the oldest phyla of eumatozoans, and some constituent groups with calcareous skeletons (corals) have contributed much to reef construction throughout geological time. The Rugosa originated in the mid Ordovician and became extinct by the end of the Permian (Hill 1981), whereas the Scleractinia have been thought to have appeared in the Triassic and now play an important role in reef construction. Corals of the Rugosa have a calcitic skeletal mineralogy and serial insertion of septa at four specific sites during their ontogeny. The Scleractinia have an aragonitic mineralogy and cyclic insertion of septa within sextants (Oliver 1980). Extinction of the Rugosa and the origin of the Scleractinia have attracted much attention, and are often discussed together. Various approaches to understanding the latter have been made, especially with Permian rugosans and Triassic scleractinians, using the criteria of septal arrangement, mode of septal insertion, fine skeletal structure, mineral composition and biostratigraphical evidence (e.g. see Schindewolf 1942; Iljina 1965, 1984; Cuif 1980; Oliver 1980; Ezaki 1989). For recent reviews, see Oliver (1980), Iljina (1984) and Sando (1993).

Many works have expanded on two conflicting views: (1) Rugosa were direct ancestors of Scleractinia ('direct-origin hypothesis') represented by Schindewolf (1942), Iljina (1965, 1984) and Cuif (1980); (2) Scleractinia originated independently of Rugosa ('independent-origin hypothesis') supported by Oliver (1980), Hill (1981) and Ezaki (1989). However, the issue remains unresolved because most interpretations have depended on circumstantial evidence such as apparent similarities or differences in morphologies and structural patterns. The absence of corals in the Lower Triassic as well as apparent differences in the ranges of Rugosa and Scleractinia have supported the idea of the independent origin of Scleractinia (Oliver 1980).

Whatever the scleractinian origin might be, both hypotheses have the common view that the Scleractinia appeared first in the Mid Triassic. Since their appearance, they have diversified into a range of environments, occasionally forming large-scale organic reefs. Four microstructural groups (fascicular, thick-trabecular, minitrabecular and pachythecal) are recognized in the Early Mesozoic Scleractinia, three of which are already found in the lower Middle Triassic (Anisian), suggesting 'polyphyletic' origins (Roniewicz and Morycowa 1993). However, molecular phylogenetic study of

the Anthozoa indicates that at least extant Scleractinia are monophyletic (Chen *et al.* 1995). Recently, a new scleractinian-like coral (*Kilbuchophyllia*) was found in the Ordovician rocks of the Southern Uplands, Scotland, and a new order Kilbuchophyllida was proposed in the Zoantharia to accommodate it (Scrutton and Clarkson 1991; Scrutton 1993). This material was interpreted as indicating a long Palaeozoic history for the anemone group, the Corallimorpharia, from which the Scleractinia were considered to have evolved in the Triassic. The phylogenetic significance of this in terms of anthozoan evolutionary patterns should attract considerable attention.

The genus *Numidiaphyllum* comprises Permian corals, having a scleractinian-like septal development (Flügel 1976) and an aragonitic skeleton (Wendt 1990*a*). Both these authors placed the genus in the Rugosa, with rugosan septal notation providing evidence for a direct-origin hypothesis. With proper understanding of its morphological characteristics and variability, it is now possible to determine whether the genus really belongs to the Rugosa.

This paper presents the ontogenetic development and intraspecific morphological variability of the type species of *Numidiaphyllum* with special analysis of the mode of septal insertion. The evaluation of the higher taxonomic position of the genus gives new insights into anthozoan phylogeny, especially that of the Zoantharia. This study also explains the mutual relationship between the end-Permian extinction of corals and a possible Triassic scleractinian origin.

MATERIALS AND FOSSIL OCCURRENCE

Mid Permian limestones, containing a highly diverse fauna and flora of calcisponges, algae, bryozoans and fusulinids (*Neoschwagerina-Yabeina* assemblage), are found in the Djebel Tebaga area of southern Tunisia (Newell *et al.* 1976). The Permian units are characterized by a reef complex, consisting of large bioherms, and are overlain by thick non-marine red-beds. Colonial coralla of *Numidiaphyllum* have been collected from Section C, west of Merbah el Oussif; the material comes from Bed 19, about 7 m thick, of the Upper Biohermal Complex (*Yabeina* Zone) of the Djebel Tebaga Reef (Newell *et al.* 1976), and was first described by Flügel (1976). Corals other than *Numidiaphyllum* have been described by Stevens (1975) and Termier *et al.* (1977).

The corallum is entirely embedded in the limestone matrix. In some cases, erosion before burial has destroyed parts of the outer wall. Corallites are rimmed with a dark micrite layer and encrusted with bryozoans and algae, forming a coral bafflestone. The coral skeleton is partly dissolved and filled with coarse, sparry calcite so that inner structures are obliterated and broken. Elsewhere, an interstitial matrix consists of brick- to yellow-coloured carbonate with irregular fenestral fabrics. More than 40 corallites were available for study. Skeletal debris includes sponges, algae, bryozoans, fusulinids, crinoid fragments, gastropods, bivalves and smaller foraminifera.

SYSTEMATIC PALAEONTOLOGY

The standard descriptive terminology for the Scleractinia (e.g. Wells 1956) is used in this account but, for better understanding of morphologies, the rugosan equivalents (e.g. Hill 1981) are indicated when necessary. A protocorallite cannot be detected in the material available, so knowledge of ontogeny (hystero-ontogeny) and septal development is based entirely on asexually reproduced corallites (hystero-corallites). Although offsets, which inherit septa from the parent, do not show the

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EXPLANATION OF PLATE 1

Polished surface of *Numidiaphyllum gillianum* Flügel, 1976; corallum is fasciculate and phaceloid. Corallites are widely spaced; Middle Permian (*Yabeina* Zone), west of Merbah el Oussif, Djebel Tebaga, southern Tunisia; × 1. 1, USNM 248224, 248229–30, 248235–36; 2, USNM 248223, 248227, 248231–34, 248237–38. For key to numbering, see Text-figure 1.

PLATE 1

EZAKI, *Numidiaphyllum*
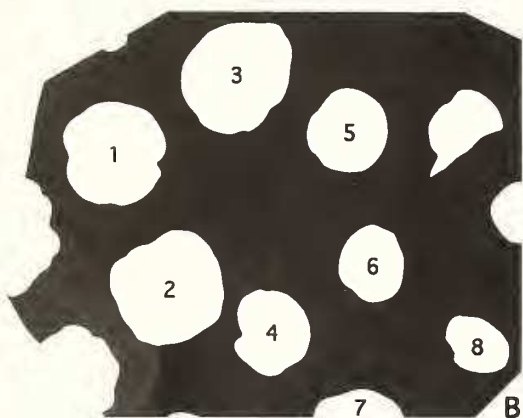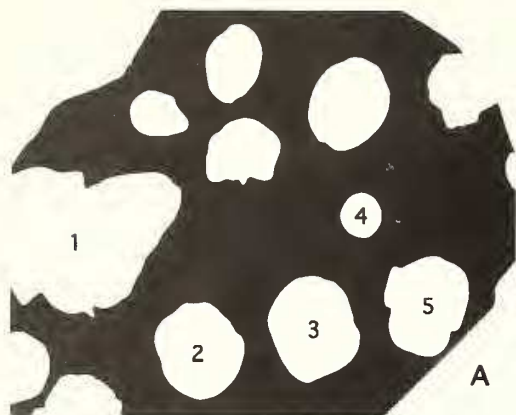
TEXT-FIG. 1. Correspondence of specimens figures in Plate 1 with registration numbers and corallites shown in Text-figures 2–3. A, 1: USNM 248229 (Text-fig. 2F), 2: USNM 248236 (Text-fig. 2B), 3: USNM 248235 (Text-fig. 2C), 4: USNM 248230 (Text-fig. 2D), 5: USNM 248224; B, 1: USNM 248237 (Text-fig. 3D), 2: USNM 248227, 3: USNM 248238 (Text-fig. 3E), 4: USNM 248223 (Text-fig. 3B), 5: USNM 248233 (Text-fig. 3C), 6: USNM 248231 (Text-fig. 3A), 7: USNM 248234, 8: USNM 248232.

initial stage of septal insertion, subsequent development is subject to the septal pattern inherent in the coral (Hill 1981). A dorso-ventral direction is not clear in the type species of *Numidiaphyllum* because (1) no protocorallites are found, and initial modes of septal insertion are unknown; (2) septa apparently show variable arrangement, although it is essentially hexameral; (3) there is no elongate or blade-like columella to indicate a plane of bilateral symmetry.

Repository of specimens. The specimens are now stored in the US National Museum of Natural History, Washington, D.C., USA (USNM).

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Phylum CNIDARIA Hatschek, 1888
Class ANTHOZOA Ehrenberg, 1834
Subclass ZOANTHARIA de Blainville, 1830
Order SCLERACTINIA Bourne, 1900
Family NUMIDIAPHYLLIDAE Flügel, 1976

Genus NUMIDIAPHYLLUM Flügel, 1976

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Type species. Numidiaphyllum gillianum Flügel, 1976.

Diagnosis. Corallum solitary(?) and fasciculate, phaceloid with aragonitic skeleton; corallites cylindrical and reproduced by intratentacular increase; walls broadly indented; six first cycle septa
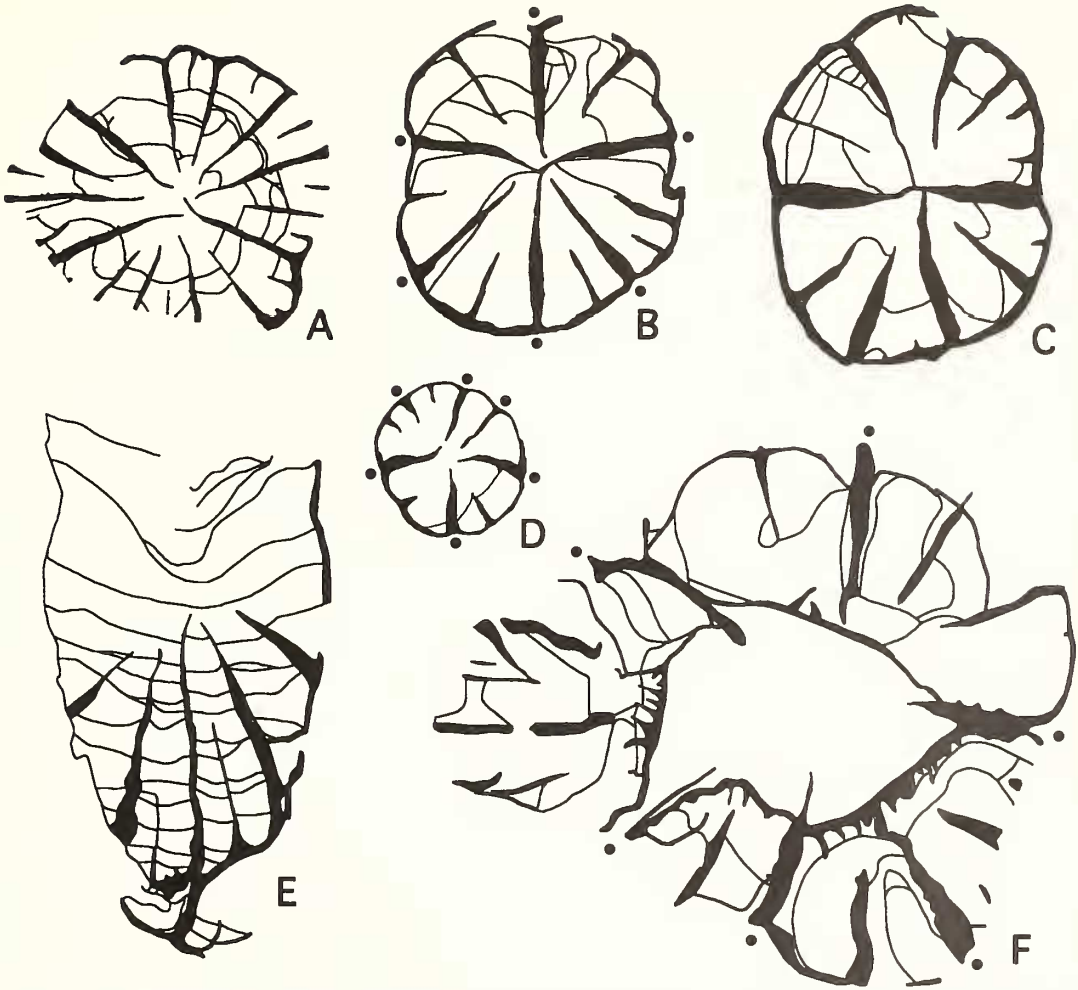
TEXT-FIG. 2. *Numidiaphyllum gillianum* Flügel, 1976; transverse features of corallites; Middle Permian (*Yabeina* Zone), west of Merbah el Oussif, Djebel Tebaga, southern Tunisia; × 1·9. A, USNM 248226; B, USNM 248236; C, USNM 248235; D, USNM 248230; E, USNM 248239; F, USNM 248229; black dots represent the six first cycle septa.

show hexameral arrangement; septa arranged radially and radiobilaterally; first order septa vary in length, and higher order septa may appear sporadically; septa granulate and showing orthogonal fine structure; neither dissepiments nor columella present.

Range. Middle Permian (*Yabeina* Zone in fusulinid zonation).

Geographical distribution. Djebel Tebaga, southern Tunisia.

Remarks. In his original description, Flügel (1976) referred to the morphological similarity between *Numidiaphyllum* and polycoeliid corals within the Rugosa, and placed *Numidiaphyllum* in his new family Numidiaphyllidae within that order. Hill (1981) doubted the suprageneric classification proposed by Flügel (1976) and preferred to assign *Numidiaphyllum* to Subclass uncertain, whereas
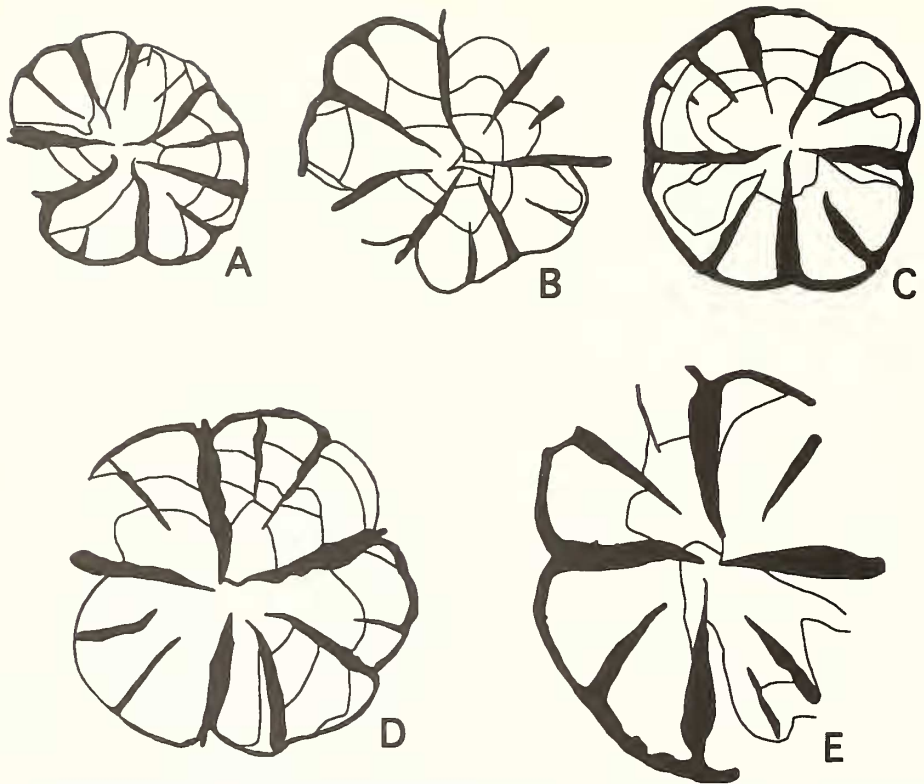
TEXT-FIG. 3. *Numidiaphyllum gillianum* Flügel, 1976; transverse features of corallites; note a marked variation in septal arrangement; for further explanation, see text; Middle Permian (*Yabeina* Zone), west of Merbah el Oussif, Djebel Tebaga, southern Tunisia; ×1·9. A, USNM 248231; B, USNM 248223; C, USNM 248233; D, USNM 248237; E, USNM 248238.

Yü *et al.* (1983) and Iljina (1984) placed it respectively in the rugosan subfamily Plerophyllinae and in the Numidiaphyllidae. Wendt (1990*a*) considered that *Numidiaphyllum* usually showed 'serial' septal insertion typical of the Rugosa, and placed the genus in the rugose family Polycoeliidae. He also suggested the primary, aragonitic composition of this 'rugosan' genus (see later) which has since been cited as strong evidence for a possible phylogenetic relationship between Palaeozoic Rugosa characterized by a calcite skeleton and the post-Palaeozoic aragonitic Scleractinia, supporting the idea of direct scleractinian origin. Nudds and Sepkoski (1993) placed Flügel's (1976) Numidiaphyllidae in Order uncertain.

The present work will demonstrate that the genus *Numidiaphyllum* has no specific morphologies that deny scleractinian affinities, and that it is a Palaeozoic representative of the order Scleractinia, not the Rugosa.
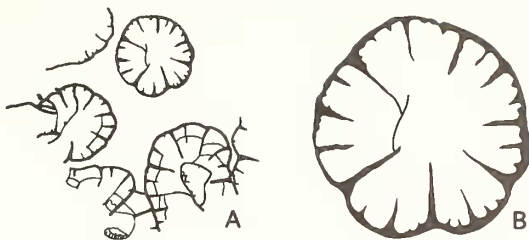
*Numidiaphyllum gillianum* Flügel, 1976

Plate 1; Text-figures 2–7

Holotype. USNM 248220, from the Middle Permian (*Yabeina* Zone), west of Merbah el Oussif, Djebel Tebaga, southern Tunisia; *paratypes.* USNM 248221–41, horizon and locality as above.

Diagnosis. Corallum solitary(?) and fasciculate, phaceloid by intratentacular tabularial increase; septa in four orders and arranged radially and radiobilaterally; septa variable in length in later

TEXT-FIG. 4. A, daughter corallites produced by intratentacular tabularial increase; × 1·2; B, close-up of a daughter corallite shown in A, indicating a hexameral septal arrangement and sporadically formed, fourth order septa, USNM 248221, × 3·3.


TEXT-FIG. 5. Polished surface of *Numidiaphyllum gillianum* Flügel, 1976, showing granulate septa on lateral surfaces; × 2.
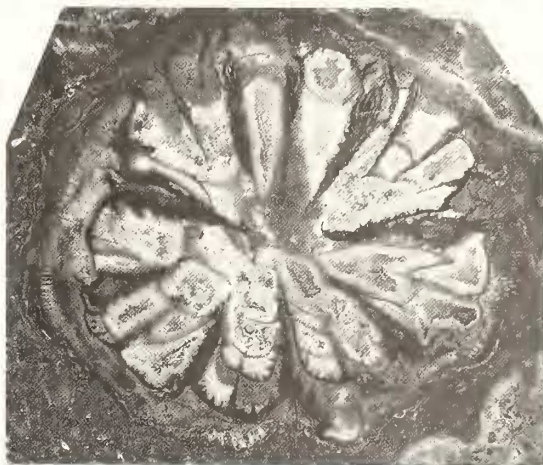
stages and higher order septa less well developed; septa variably granulate; no dissepiments or columella.

Description. The corallum is solitary(?) and fasciculate, phaceloid (Pl. 1). Corallites are cylindrical, ranging from 8·9 to 38 mm in diameter (average 20 mm), and widely spaced without connecting processes. About ten corallites occur within 0·01 square metres in transverse section. No corallite outer-surfaces are observed. The wall is generally thin and broadly embayed at joints with septa (Text-figs 3B–C, 6M–N). Asexual reproduction occurs by means of tabularial increase (Text-figs 2F, 4A). Corallites are circular to elliptical in transverse section. Septa are in four orders, but the fourth order septa appear only in some loculi. Septa are arranged radially, essentially showing a hexameral arrangement with six first cycle septa (Text-figs 2B, D, 4B, 7). A radio-bilateral symmetry is also achieved by an undeveloped protoseptum and/or accelerated or retarded insertion of septa (Text-fig. 3C–D). There are 18 septa in a corallite at a diameter of 19 mm. The first order septa taper axially leaving an open space, but may be spindle-shaped, tapering towards the wall. They are slightly flexuous and occasionally conjoined axially without forming a columella. No specific septum is lengthened preferentially. Apart from the six first cycle septa, the septa may be long and almost equal in length. The second order alternates with the first order, though not always, and is variable in length up to 80 per cent. of the corallite radius. The third order septa originate between neighbouring first and second order septa. The fourth order septa occur sporadically and are present as ridges (Text-figs 4B, 7C). Septa are granulate on lateral surfaces (Text-figs 2A, 5) and are rarely carinated. The dilated, first order septa delimit parricidal daughter corallites (Text-fig. 2F). The fine skeletal structure is obscure due to recrystallization, although relics of orthogonal (fibro-normal) structure may be traced near the septal periphery (Wendt 1990a, fig. 1-4; 1990b, fig. 6E). Tabulae are complete and irregularly spaced. They are concave upwards to various degrees, but may be slightly convex peripherally (Text-fig. 2E). Five to seven tabulae are counted in a vertical distance of 10 mm. Transversely cut edges of tabulae are seen in interseptal spaces, showing a concentric and herringbone arrangement. Neither dissepiments nor columella are present.
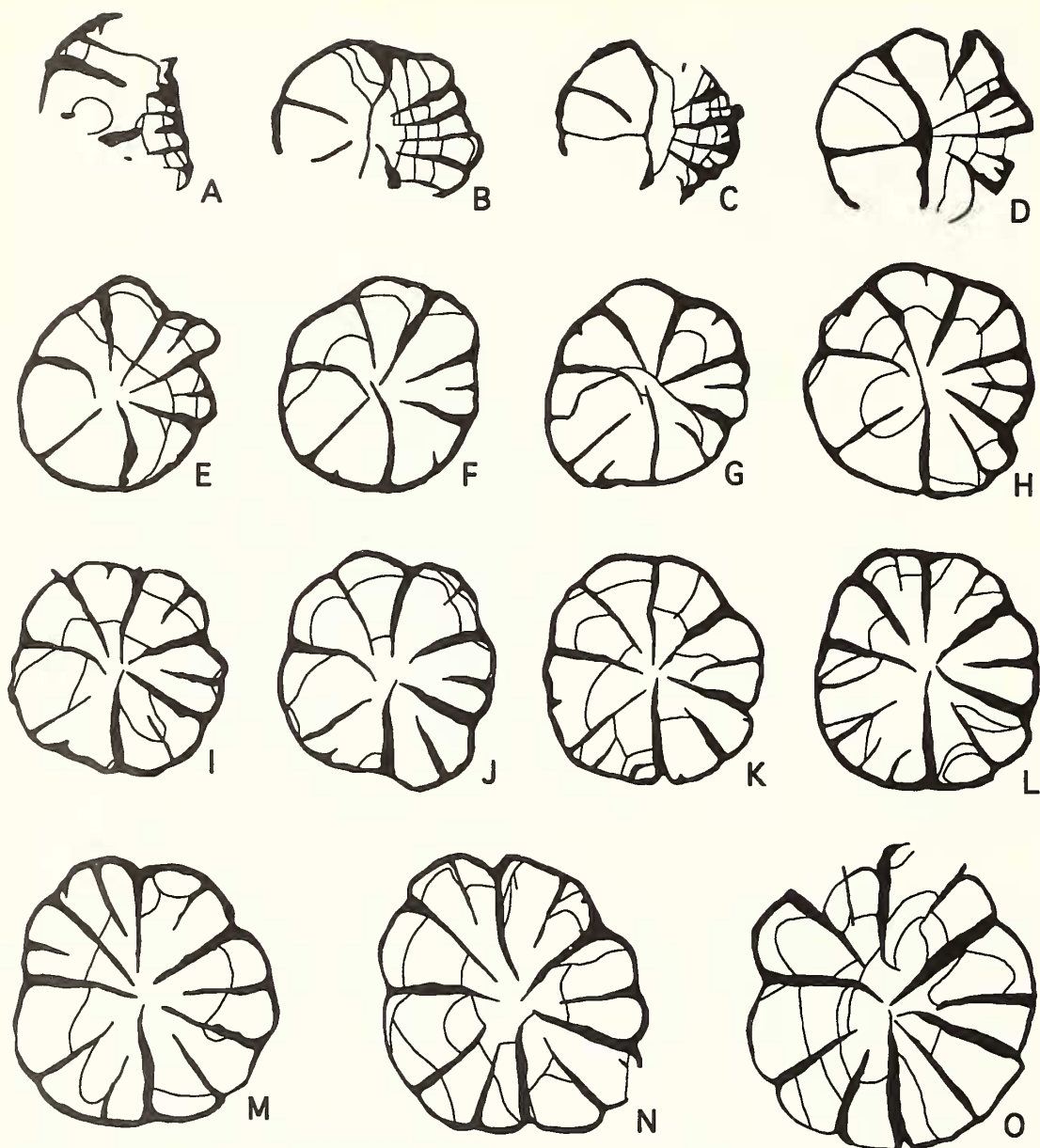
TEXT-FIG. 6. *Numidiaphyllum gillianum* Flügel, 1976. Serial transverse features of the holotype, showing ontogenetic development of septa and septal arrangement. Note a high variability in length of second order septa and walls embayed at joints with septa. For further explanation, see text; Middle Permian (*Yabeina* Zone), west of Merbah el Oussif, Djebel Tebaga, southern Tunisia, USNM 248220; × 1·8.

Mode of asexual reproduction and ontogeny. Offsets originate in the tabularial part, and some of the first order septa become the dividing walls of daughter corallites, together with the walls formed at the axis (Text-fig. 2F). Parricidal offsets are separated and replace the parent corallite. Each daughter corallite inherits the old septa of the parent corallite (atavo-tissue) at its periphery and adds new septa of its own (neo-tissue) on the opposite side. Text-figure 6 shows the ontogenetic

morphological changes of a daughter corallite which was reproduced by means of tabularial increase.

In cases of tabularial increase, septal length in the daughter corallite is somewhat irregular at first. The septa are less developed on the dividing walls and in the atavo-tissue (Text-figs 2F, 6A). They are not differentiated in length and thickness in the neo-tissue (Text-figs 2F, 6A–B), where transversely cut edges of tabulae are present in a concentric arrangement. The second order septa are inserted between the first order septa, and the third order septa appear between the undifferentiated first order and second order septa (Text-fig. 6C). The septa taper axially with a thickened corallite wall. At a later stage (Text-fig. 6D), they are much differentiated in length, though variable, taking on an apparently radial symmetry. The third order septa then disappear and are restricted to the wall (Text-fig. 6E). In the following stage (Text-fig. 6F), seven septa are developed and, when present in an interseptal space, the second order septa are short. As a corallite grows, it maintains a similar appearance with its essential features unchanged but with second order septa of variable length. An almost completely radial arrangement appears with the axial elongation of the second order septa (Text-fig. 6O). The third order septa occur sporadically as low ridges.

Septal insertion. By tracing each individual septum in serial transverse sections, allowing for the effects of septal stunting (see Weyer 1972), the mode of septal insertion (timing, location and order) can be determined. It is difficult to discern the initial mode of septal insertion in *N. gillianum* because daughter corallites are produced asexually by intratentacular tabularial increase.

Flügel (1976) mentioned that metasepta of *N. gillianum* originated in an irregular manner. Wendt (1990a) considered that septa were produced 'serially' in a polycoeliid manner characteristic of the Rugosa. However, the 'first pair of metasepta' (Wendt 1990a, fig. 2-4) are not the first appearing metasepta (*sensu* Rugosa), but part of the higher orders of septa (*sensu* Scleractinia), although the septa designated as cardinal, counter, two alar and two counter-lateral correspond to the first cycle septa.

In *N. gillianum*, the fourth order septa are present sporadically as low ridges (Text-figs 2A, 4B). Six first cycle septa are present, and the six septa divide the corallite into sextants for subsequent septal insertion, resulting in a hexameral septal arrangement (Text-fig. 7). Although the daughter corallites inherit some septa from the parent corallites and septa are occasionally retarded and/or accelerated in insertion, higher orders of septa, up to the fourth order, appear between neighbouring lower orders of septa in each sextant. Hence the second order septa are inserted between the first order septa, and third order septa appear between first order and second order septa in succession (Text-figs 6B–D, 7D–F). These features of septal arrangement and insertion strongly indicate an affinity close to the Scleractinia because the Scleractinia have six protosepta regulating the locations of subsequent septal insertion in cyclic fashion (Wells 1956).

Variability. Growth forms of the corals are solitary(?) and fasciculate, phaceloid. In corallites with a fourth order of septa, corallite diameter varies, ranging from 8·9 to 38 mm. Septal insertion is apparently incomplete because some higher order septa do not appear and are restricted to the wall. Septa are highly variable in length throughout corallite growth. The fourth order septa occur only sporadically. The timing and degree of septal stunting and withdrawal, especially of higher order septa, may be related to the formation of tabulae. Septa are granulate on lateral surfaces in some corallites (Text-figs 2A, 5) but are smooth in other corallites. Septa are variably dilated, tapering and fusiform.

Septal arrangement is essentially hexameral, with six first cycle septa (Text-figs 2B, 7F), and is more evident in younger corallites (Text-figs 2D, 4B). However, this varies among individuals, especially in later stages. Septa are not always developed equally within a corallite. Corallites take on tetrameral (Text-fig. 3E) and pentameral structure showing a bilateral symmetry (Text-fig. 3C–D), due to an underdevelopment of first order septa and/or a retardation of septal insertion on one side. Later, this pattern may be hexameral with the introduction of the higher orders of septa in retarded
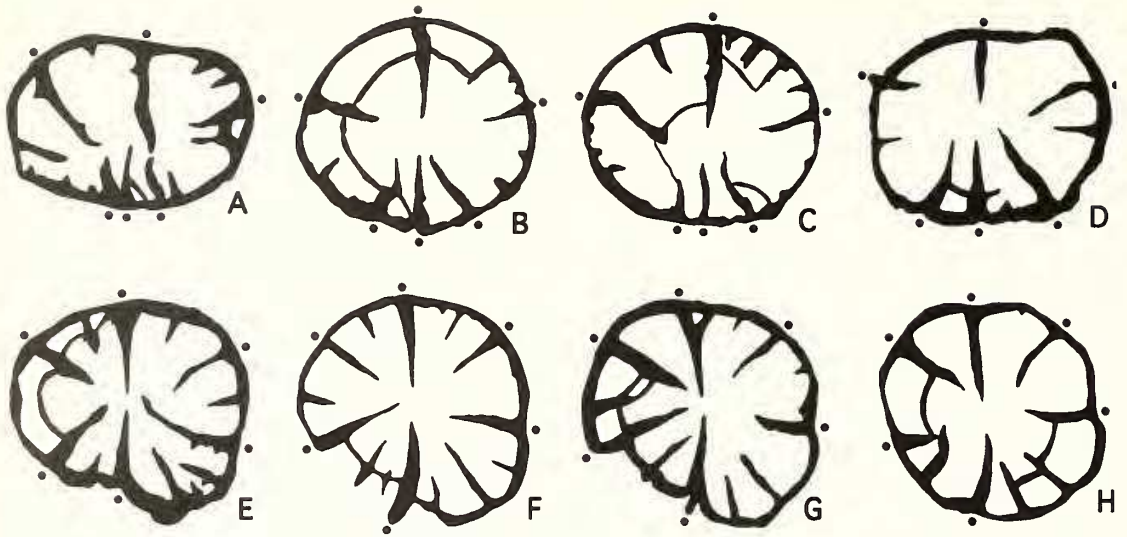
TEXT-FIG. 7. *Numidiaphyllum gillianum* Flügel, 1976. Serial transverse features of daughter corallite, showing ontogenetic development of septa and septal arrangement. Septa may show a bilateral symmetry but are later characterized by a hexameral symmetry. Septa are highly variable in length throughout growth. Black dots represent the six first cycle septa. For further explanation, see text; magnification unknown (modified after Wendt 1990a).

sextants (Text-fig. 7F). Others seemingly show heptameral (Text-fig. 6) or octameral structure, with one or two additional, elongated septa probably of second cycle origin. The septal arrangement is thus variable throughout ontogenetic (growth) stages. Septal dilation at the time of intratentacular tabularial budding may also be related to the apparent variation in septal arrangement. A corallite that is elongate and/or elliptical in outline, resulting from oblique sectioning, original shape, or compaction commonly shows septal acceleration in the end sextants (Wells 1956, fig. 240B).

When intratentacular increase occurs, offsets are separated by dilated first order septa of the parent corallite and by new walls in the tabularium. The parent corallites are divided into several daughter corallites which are outlined irregularly at first (Text-figs 2F, 4A), with septa not clearly differentiated in length and thickness. Septal insertion is retarded on the dividing walls and in the atavo-tissue. Some variability, including septal length, arrangement and thickness, is also induced by intratentacular asexual reproduction.

Remarks. N. gillianum is similar to the Triassic scleractinian *Stylophyllopsis zitteli* described originally by Frech (1890) from the Rhaetian of the Zlambach Beds at Fischerwise, Austria. Both species show hexameral septal arrangement, especially in younger corallites, and granulation of septa. Seemingly large morphological variability in septal length, thickness and development is also commonly observed. However, *N. gillianum* lacks septal spines, even in the calicular part, as well as dissepiments. It shows an orthogonal fine structure of septa (Wendt 1990a, 1990b), but its relationship to the fascicular type characteristic of *Stylophyllopsis* (see Cuif 1972; Roniewicz and Morycowa 1993) is uncertain.

N. gillianum is akin to the Triassic scleractinians *Volzeia fritschi* and *Protoheterastraea leonhardi* in hexameral septal arrangements and septal development during the course of ontogeny. However, it is separable from these two species by sporadically distributed higher orders of septa and the absence of dissepiments.

SKELETAL COMPOSITION AND PALAEOENVIRONMENTS

The skeleton of the corals here studied is composed of a fine- to coarse-grained mosaic of neomorphic calcite interpreted as being converted from aragonite. The septa may be rimmed with a micritic envelope cemented by rinds of acicular calcite. Interseptal voids are filled with coarse, mosaic spar (Wendt 1990*b*, fig. 5E–F). Wendt (1990*a*) showed high Sr^{++} values in calcitized *Numidiaphyllum* skeletons from Tunisia, and the present author follows Wendt's (1990*a*, 1990*b*) conclusion that the original skeleton of this genus was aragonitic, although X-ray diffraction analysis shows no aragonite peak. In Tunisia, aragonitic mineralogies are still preserved in some reef components (Wendt 1977). Aragonite precipitation from seawater is kinetically favoured at higher temperature, higher Mg^{++} and lower Pco_2 levels, and other complex chemical conditions (Tucker and Wright 1990, p. 409).

In the Mid Permian limestones of southern Tunisia, *Numidiaphyllum* occurs where a highly diverse biotic association dominated by calcisponges and algae has been recognized (Newell *et al.* 1976; Senowbari-Daryan and Rigby 1988). A specific biotic community, shown by a calcisponge-algal association, was apparently crucial to the first appearance and survival of *Numidiaphyllum* which lived both as a dweller and baffler in warm-water sponge-algal reefs in tropical latitudes.

SCLERACTINIAN AFFINITY OF *NUMIDIAPHYLLUM*

On both age and mineralogical criteria, *Numidiaphyllum* could be considered (1) as merely a variant within the Rugosa, or (2) as a precocious scleractinian. Septa are marked on the corallite wall by distinct indents (Text-figs 3C, 4B, 6M–N), like the septal grooves which characterize Rugosa, not by costae as typify Scleractinia. However, such septal indents are also found in the scleractinian *Stylophyllopsis mucronata* from the Lower Jurassic of Britain (Duncan 1867). Septal faces are granulate to various degrees. Six first cycle septa divide the corallite in sextants, and subsequent second and third cycle septa are inserted in each interseptal space, showing a hexameral, cyclic insertion. The mode of septal insertion, the most important character for judging suprafamilial position, is like those in the Scleractinia. Intratentacular tabularial increase is a mode of asexual reproduction, and a similar mode is found not only in Rugosa (e.g. *Entelophyllum articulatum*), but also in Scleractinia (e.g. *Stylophyllopsis rudis* and *Volzeia fritschi*).

The weight of evidence indicates that *Numidiaphyllum* is neither a rugosan variant, regardless of its occurrence in the Permian, nor a representative of an intermediate group between Rugosa and Scleractinia; the latter has been erroneously suggested for Permian corals showing occasional irregular septal insertion (Schindewolf 1942; Iljina 1965, 1984). See Oliver (1980) and Ezaki (1989), for further discussion.

The question to be addressed is therefore what is the higher taxonomic position of this Permian scleractinian-like coral with an aragonitic composition.

ANTHOZOAN PHYLOGENY AND TRIASSIC SCLERACTINIAN ORIGINS

Palaeozoic scleractinian-like corals have been reported from the middle Ordovician (Erina and Kim 1980; Scrutton and Clarkson 1991; Scrutton 1993), and the genus *Kilbuchophyllia* shows scleractinian affinity on the basis of latex replicas of the microarchitecture of the skeletal elements and septal pattern (Scrutton and Clarkson 1991). *Kilbuchophyllia*, in the new order Kilbucho-phyllida, was interpreted by those authors as being an early example of skeletonization from among a group of sea-anemones which were possible ancestors of the Triassic scleractinians. Apart from *Kilbuchophyllia*, Palaeozoic scleractinian-like corals so far recognized were reviewed briefly by Scrutton and Clarkson (1991) and shown to be unacceptable or too poorly known. *Kilbuchophyllia* is the only suitable Palaeozoic subject for this comparison. It must be decided whether

Numidiaphyllum, with a basic, scleractinian body plan, should be allied to the Kilbuchophyllida or the Scleractinia.

Scleractinian-like corals occur in both the Ordovician and Permian, showing the persistence of zoantharians with a scleractinian body plan, even in the barren intervals during Silurian to Carboniferous times, a time duration of at least 150 My. The absence of undoubted scleractinian-like corals for such a long period and, moreover, a close morphological similarity to some Triassic scleractinians (see remarks in Systematic Palaeontology and Scleractinian Affinity of *Numidia-phyllum*), suggest a more likely placement of the Permian *Numidiaphyllum* with the Scleractinia rather than the Kilbuchophyllida.

A large number of skeletonized benthic organisms became extinct at the end of the Permian in the severest extinction of Phanerozoic time (e.g. Sepkoski 1989; Erwin 1993, 1994), and no Early Triassic corals are known. It may seem surprising that the new genus *Numidiaphyllum* originated during the late Mid Permian, when rugose and tabulate corals greatly declined phylogenetically into the end-Permian extinction. The Late Permian decline and disappearance of the Rugosa occurred via morphological changes, from complex to simple forms, reflecting phylogenetic trends and differential deteriorating environments (Ezaki 1993, 1994). Fasciculate rugose corals survived up to the latest Permian Changxingian but became extinct by the end of the period (Ezaki 1994). The appearance of *Numidiaphyllum* with an aragonitic skeleton, might not have an immediate causal relationship with the decline of rugose and tabulate corals. It lived in exceptionally favourable warm-water conditions.

No evidence has been found of reefs in the Early Triassic oceans, when protracted inhibiting conditions for reef-forming organisms prevailed (Stanley 1988). The Permian survivors, characterized by calcisponges and algae, were considered to have played a crucial role in the re-establishment of reefs in the Mid Triassic after a period of global reef-gap (Stanley 1988; Hallam 1991). If the Scleractinia did not possess zooxanthellae until the Late Triassic (Stanley and Swart 1995), azooxanthellate zoantharians with a basic, scleractinian body plan could have grown in 'deep-water' settings during the Early Triassic reef-gap period. Whatever their variation might be, the zoantharians, which may be closely related to *Numidiaphyllum*, survived the disastrous end-Permian extinction in refuges. With global removal of inhibiting factors everywhere in the Anisian ocean (see Ezaki 1995), as well as regional amelioration of substrate conditions, scleractinian corals dominated in association with calcisponges and algae. Geochemical seawater conditions also favoured aragonite-secreting organisms during Triassic times (Railsback and Anderson 1987). The difference in basic body plan between the Rugosa and the Scleractinia was not established around the time of the Permian–Triassic boundary but already in Early Palaeozoic times. Whatever the origin, Scleractinia have no immediate phylogenetic relationship to Rugosa, arguing against the direct-origin hypothesis.

CONCLUSIONS

The end-Permian extinction played a significant role in anthozoan evolutionary patterns because the Rugosa and the Tabulata became extinct. However, the zoantharians with a basic, scleractinian body plan survived and gave rise to Triassic scleractinian ancestors. The taxonomic reinterpretation of the Permian coral *Numidiaphyllum* provides a clearer scenario for anthozoan phylogeny in terms of the end-Permian extinction and the origin of Triassic Scleractinia.

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